PREY SELECTION BY THE NEOTROPICAL ROBBER FLY, *ATRACTIA MARGINATA* (DIPTERA: ASILIDAE)

TODD E. SHELLY

Department of Biology, University of California, Los Angeles, California 90024.

Abstract.—Actual prey of *Atractia marginata* Osten Sacken were compared to sticky trap samples of available prey. Individuals did not feed randomly on available prey. Coleoptera were overrepresented in the diet in comparison to their contribution to the sticky trap sample, while the opposite was true for Isoptera and non-nematocerous Diptera. In addition, foraging rate was found to vary directly with prey abundance. In a comparison of two adjacent microhabitats, both total prey abundance and foraging rate of *A. marginata* were approximately three times greater in one area than in the other.

Many researchers have recorded prey of adult robber flies. These reports range from anecdotal accounts in which only one or several prey are recorded (Wallis, 1913; Balduf, 1943; Hardy, 1953; Bouseman and Maier, 1977) to intensive studies in which hundreds or even thousands of prey are listed for individual asilid species (Adamovic, 1963, 1968; Dennis and Lavigne, 1975; Scarbrough, 1979; Scarbrough and Sraver, 1979). Despite this variation, these studies all share a common feature, i.e., actual prey were collected without regard to the availability of prey in the habitat. Thus, while investigators have made inferences concerning apparent preferences for particular prey types and sizes, the actual extent to which any asilid species selectively feeds upon particular prey remains unknown. The use of lures of varying dimensions and colors may help identify those prey characteristics most likely to elicit an asilid attack response (Lavigne and Holland, 1969; Dennis et al., 1975; Shelly and Pearson. 1978, 1980), but clearly a comparison of actual prey vs. available prey constitutes the most direct analysis of prey selection.

In this paper I compare the actual prey of a Neotropical robber fly species with samples of available prey obtained using sticky traps. *Atractia marginata* Osten Sacken is a small (8 mm–10 mm) robber fly recorded from forests in Panama, Costa Rica, and Nicaragua (E. Fisher, personal communication). Like most robber flies, *A. marginata* is a sit-and-wait predator. Individuals usually perch on the sides of fallen trees and attempt aerial capture of flying insects. Upon successful capture, the asilid returns to its perch and sucks the contents of its prey. Collection of prey from feeding individuals thus permits direct assessment of the dietary composition.

Preliminary observations also suggested that *A. marginata* individuals within meters of one another foraged at greatly different rates. By identifying sites of "high" and "low" foraging activity and measuring prey abundance within each,

it was possible to test the hypothesis that foraging rate is directly proportional to the encounter rate with available prey. This relationship has been observed for other predaceous insects (Hassell et al., 1976) but has never been documented for robber flies.

MATERIALS AND METHODS

The study was conducted between February 26 and March 11, 1979, on Barro Colorado Island (BCI), Panama. This time interval coincided approximately with the mid-point of the dry season, which annually extends from late December to early May (Croat, 1978). No rain fell during the course of the study, and days were generally sunny. BCI is covered by a lowland tropical moist forest (Holdridge et al., 1971) portions of which range in age from approximately 60–130 years (Croat, 1978; Knight, 1975).

All observations and collections were made at one fallen tree within the forest. The tree was approximately 20 m long and 1.5 m in circumference. A bend in the trunk resulted in the fallen tree having the shape of an inverted V with its apex off the ground and its arms sloping downward until they were lying on the ground. Preliminary observations indicated that *A. marginata* perched near the apex were foraging less frequently than were individuals perched along the arms and hence closer to the ground. To investigate this difference, I first established a high and a low trunk section and then (1) measured foraging rates of *A. marginata* and (2) sampled actual and available prey in each section.

The trunk sections were established as follows. The "high" section included the apex of the fall (tree underside 91 cm above ground) and a 1.75 m length immediately to the left of the apex (tree underside 71 cm above ground at the lowest point) and a 1.0 m length immediately to the right of the apex (tree underside 84 cm above ground at the lowest point). The low section was a 3.0 m portion of the right arm of the fall that rested directly on the ground. Only 5.1 m separated the high and low sections. No low section was established on the left arm owing to the presence there of an active nest of *Trigona* sp. (Hymenoptera: Apidae). Although no capture attempts were observed, individuals of *A. marginata* in the nest's vicinity were observed chasing bees. The *Trigona*-induced flights thus precluded valid comparisons with *A. marginata* individuals in nest free portions of the trunk.

All foraging observations were made between 1200–1600 hrs between February 26–March 2 and March 8–March 11. In general, 3–5 females were observed each day in both sections. During the entire study, 30 females were observed in each section. These observations consisted of watching a female for 5 minutes and recording the number of foraging flights. Only females were observed since (1) females were much more abundant than males and (2) I wished to avoid potential complications arising from sexual differences in behavior. Foraging flights were easily distinguished from other flights (e.g. relocation flights), since (1) the prey eliciting the attack could often be seen and (2) they were characteristically rapid, straight flights to points 15 cm–45 cm from the log surface. In addition, after a foraging flight, the individual generally returned to a site very close to its original position. If, however, an individual moved out of the study section (through either a foraging or relocation flight), observation ceased. In addition to flight activity,

foraging efficiency (no. successful captures/no. foraging flights) was noted. Observation did not stop following a successful capture, since feeding individuals usually continued to search for prey.

Actual prey were collected during the same time intervals in which foraging observations were made. *Atractia marginata* females with prey were captured by a quick "cupping" action of a wide-mouthed jar over the asilid. After the asilid dropped its prey, the prey was collected, and the asilid was released. Prey were identified to order except for Diptera which were further categorized as nematocerans or non-nematocerans. Body lengths were measured to the nearest 0.1 mm using a dissecting microscope equipped with a disc micrometer.

Available prey were sampled at both trunk sections from March 3–March 7. Ideally, samples of available and actual prey would be taken simultaneously. Over several hours, however, my movements would possibly affect insect distribution near the fallen tree. Consequently, after setting the traps, I avoided the area. I must assume, then, that these samples of available prey were typical of the entire study period. Two tangle-foot coated, white paper discs (diameter 11.5 cm) were placed at each section at 1200 hrs and removed at 1600 hrs. Each disc was fastened to the top of a wooden rod which in turn was driven into the ground immediately adjacent to the log with its plane perpendicular to the log's long axis. The discs in the high and low sections were positioned with their centers 115 cm and 95 cm above ground and 20 cm and 25 cm above ground, respectively. As with actual prey, sampled insects were identified to order except for Diptera which were further categorized as nematocerans or non-nematocerans. Body lengths were measured to the nearest 1 mm with a ruler. Entrapment in the tanglefoot precluded more accurate measurement of the sampled items.

Actual prey of *A. marginata* females were compared with the sticky trap sample in two ways. Differences in the taxonomic and size compositions of the actual and available prey were first tested using a G-statistic (Sokal and Rohlf, 1969: 575). Ivlev's (1961) index of electivity (E) was also used as a measure of prey selectivity: $E = (r_i - p_i)/(r_i + p_i)$ where r_i is the proportion of the predator's diet composed of prey type (or size) category i, and p_i is the proportion of the available prey composed of prey type (or size) category i. Values of E range from +1.0 (complete preference) to −1.0 (complete avoidance).

<center>RESULTS</center>

Atractia marginata females within the high trunk section foraged less frequently than did females in the low section. For the 30 females observed within each section, the mean foraging rates were 0.42 (SD = 0.28) and 1.29 (SD = 0.55) flights/minute for the high and low sections, respectively ($t = 7.64$, $P < .001$). Although flight activity varied, foraging efficiencies did not differ significantly between females in the two sections ($t = 0.12$, $P < .9$; arc sine transformation, Sokal and Rohlf, 1969: 608). The foraging efficiencies for the high and low sections were 6.0% (4/67) and 6.6% (13/196), respectively.

Prey abundance also differed greatly between the high and low trunk sections (Table 1). Nearly 3 times as many insects were collected at the low section (mean number/disc = 31.2, SD = 6.5) than at the high section (mean number/disc = 12.4, SD = 2.5). These means were significantly different ($t = 8.6$, $P < .001$). Despite this numerical difference, taxonomic composition of the samples did not

Table 1.   Taxonomic composition of available and actual prey of *Atractia marginata* females. Available prey values for each section represent total number of individuals of each category collected on 10 sampling discs over a 5 day period.

Prey taxa	Available prey						Actual prey		
	Low trunk section		High trunk section		Total				
	No.	(%)	No.	(%)	No.	(%)	No.	(%)	Electivity
Coleoptera	148	(47.4)	64	(51.6)	212	(48.6)	75	(69.4)	+0.18
Diptera									
Nematocera	43	(13.8)	16	(12.9)	59	(13.5)	13	(12.0)	−0.06
Non-Nematocera	61	(19.5)	22	(17.7)	83	(19.0)	8	(7.4)	−0.44
Isoptera	26	(8.3)	17	(13.7)	43	(9.9)	6	(5.5)	−0.28
Other	34[1]	(10.9)	5[2]	(4.0)	39	(8.9)	6[3]	(5.5)	—
Total	312		124		436		108		

[1] Other includes: 20 Hymenoptera, 7 Thysanoptera, 5 Homoptera, 1 Hemiptera, 1 Lepidoptera.
[2] Other includes: 3 Hymenoptera, 1 Homoptera, 1 Strepsiptera.
[3] Other includes: 3 Hymenoptera, 1 Homoptera, 2 Psocoptera.

differ significantly between the 2 sections (G = 8.2, $P < .1$, df = 4). In both sections, Coleoptera (primarily Platypodidae and Scolytidae) and Diptera represented approximately 50% and 30% of the sampled prey, respectively. Among the Diptera, approximately 40% were nematocerans (primarily Sciaridae and Cecidomyiidae) and 60% were non-nematocerans (primarily Phoridae and Stratiomyidae) in both sections. Similarly, Isoptera comprised approximately 10% of the trapped insects in both sections. In addition to this taxonomic similarity, size frequency distributions of Coleoptera (G = 3.2, $P < .5$, df = 5) and Diptera (G = 2.4, $P < .1$, df = 3 for nematocerans and non-nematocerans combined) did not differ significantly between the high and low sections. Given these similarities in available prey in the 2 sections, the following comparisons between actual and available prey were made using combined data from both sections.

The recorded prey of *A. marginata* females did not represent a random sample of the available prey (G = 18.0, $P < .001$, df = 4, Table 1). Coleoptera comprised a much greater proportion of the diet (69.4%) than of the sampled prey (48.6%). Consequently, the electivity value for Coleoptera was positive. As in the sticky trap sample, the majority (approximately 75%) of beetle prey were scolytids and platypodids. In contrast, both non-nematocerous Diptera and Isoptera were underrepresented in the diet relative to their contributions to the sample of available prey. As a result, electivity values for these prey were negative. Nematocerous Diptera, on the other hand, were consumed in approximately the same proportion as their relative abundance in the environment, and the corresponding electivity value was near zero.

Only Diptera and Coleoptera were preyed upon in sufficient numbers to permit a valid comparison between actual and available prey size distributions (Table 2). These distributions differed significantly for both dipteran prey (G = 16.4, $P < .001$, df = 3 for nematocerans and non-nematocerans combined) and beetles (G = 17.6, $P < .005$, df = 5). For both taxa, the smaller size classes were overrepresented in the diet relative to their contributions to the sticky trap sample. Electivity values were positive for flies less than 2 mm but negative for larger

Table 2.   Size distributions of available and actual prey. Numbers of available prey represent total numbers of each size class collected on 20 sampling discs over a 5 day period. Nematocera and non-Nematocera are combined in Diptera figures.

Prey	Size (mm)	Available		Actual		Electivity
		No.	(%)	No.	(%)	
Diptera	0–1	18	(12.7)	4	(19.0)	+0.20
	1–2	55	(38.7)	12	(57.1)	+0.19
	2–3	46	(32.4)	5	(23.8)	−0.15
	>3	23	(16.3)	0	(0.0)	−1.00
Coleoptera	0–1	15	(7.1)	6	(8.0)	+0.06
	1–2	50	(23.6)	18	(24.0)	+0.01
	2–3	92	(43.3)	40	(53.3)	+0.10
	3–4	20	(9.4)	10	(13.3)	+0.17
	4–5	21	(9.9)	1	(1.3)	−0.77
	>5	14	(6.6)	0	(0.0)	−1.00

flies. Similarly, electivity values were positive for beetles less than 4 mm but negative for the larger size classes. Among beetle prey, a sharp decrease in electivity was noted between the 3 mm–4 mm and 4 mm–5 mm size classes. Both classes comprised approximately 9% of the available beetle prey, but 3 mm–4 mm and 4 mm–5 mm individuals comprised 13.3% and 1.3% of the actual beetle prey, respectively.

DISCUSSION

Field studies of prey selection invariably rely upon sampling methods which yield biased estimates of both actual and available prey. Sticky traps, for example, have an inherent bias resulting from the fact that different insects have different abilities to detect and avoid a trap (examples in Robinson and Robinson, 1973). In addition, Olive (1980) suggested that very small insects may be passively carried around traps by air currents and hence be underrepresented in the sample. The sampling of actual prey is subject to a "handling time" bias. That is, small prey that are rapidly consumed are less likely to be sampled than are larger items that require longer processing times. Since the effect of any of these biases is unknown in the present study, the following interpretations must be considered preliminary. More definitive statements may require correction for these biases through simultaneous use of several sampling methods (e.g. Taylor, 1962).

The present results suggest that *A. marginata* females did not feed randomly upon available prey. Two explanations may account for this finding. First, *A. marginata* females may have restricted attacks to those prey offering a "reasonable" chance of capture, but, within this subset, attempted capture of every prey encountered. Dietary composition may thus have reflected only differential capture probabilities for different types and sizes of "catchable" prey. Second, within the "catchable" subset of available prey, *A. marginata* females may have further restricted attacks to those prey yielding maximum rates of net energy intake. The foraging behavior of several insect predators (Charnov, 1976; Townsend and Hildrew, 1980) appears consistent with the predictions of optimal diet theory (review in Pyke et al., 1977). Consequently, dietary composition may have re-

flected not only differential capture probabilities, but also active discrimination within the subset of "catchable" prey.

While a rigorous assessment of these explanations is not possible, several observations suggest that differential prey vulnerability is a primary determinant of dietary composition. *Atractia marginata* females did not attempt capture of all sighted prey, e.g. large, fast flying prey such as euglossine bees and butterflies occasionally flew near an asilid but usually failed to elicit an attack response. Such prey were presumably ignored, since they offered only minimal chance of successful capture. The positive electivity found for Coleoptera and the difference in the electivity values noted between nematocerous and non-nematocerous Diptera are consistent with my subjective assessment of the relative vulnerability of these groups. A combination of slow and relatively straight flight may have rendered beetles more susceptible to predation. Most Diptera, if not faster fliers, appeared to have erratic flight paths and consequently may have been more difficult to capture. However, the slow flying nematocerans may have been more easily captured than the non-nematocerans (e.g. phorids and stratiomyids), which are probably more rapid fliers. Finally, the negative electivity values found for the larger beetles and flies are consistent with the assumption (Hocking, 1953) that, within a prey taxon, larger individuals are more rapid fliers and hence more difficult to capture and subdue than smaller individuals.

Prey density has often been considered an important determinant of robber fly foraging activity (Lavigne and Holland, 1969; Dennis and Lavigne, 1975; Scarbrough and Norden, 1977). However, quantitative evidence has been lacking. The present results indicate that the foraging rate of *A. marginata* females varied directly with prey abundance. Total prey abundance and foraging rate were approximately 3 times greater in the low section than in the high section. Interestingly, despite higher prey abundance in the low section, females did not exhibit an "aggregative response" (Hassell et al., 1976). That is, females did not appear to concentrate their foraging efforts in the area with greater prey density. Females could always be found in both sections, and no clustering of individuals in the low section was ever apparent. While air temperature and light levels appeared identical in both sections, it is possible that factors unrelated to prey density (e.g. aggressive encounters among females) affected the distribution of females along the log.

Literature Cited

Adamovic, Z. R. 1963. The feeding habits of some asilid species (Asilidae, Diptera) in Yugoslavia. Arh. Biol. Nauka 15: 41–74.
———. 1968. Feeding-habits of some robber flies preying upon Orthoptera. Ekologiya 3: 119–132.
Balduf, W. V. 1943. New food records of entomophagous insects. Entomol. News 54: 12–15.
Bouseman, J. K. and C. T. Maier. 1977. The robber fly *Proctacanthus hinei* Bromley (Diptera, Asilidae) in Illinois, with records of bumblebees as prey (Hymenoptera: Apoidea). J. Kans. Entomol. Soc. 50: 357–358.

Charnov, E. R. 1976. Optimal foraging: attack strategy of a mantid. Am. Nat. 110: 141–151.

Croat, T. B. 1978. Flora of Barro Colorado Island. Stanford Univ. Press, Stanford. 943 pp.

Dennis, D. S. and R. J. Lavigne. 1975. Comparative behavior of Wyoming robber flies. II. (Diptera: Asilidae). Univ. Wyo. Agric. Exp. Sta. Sci. Monogr. 30: 1–68.

Dennis, D. S., G. P. Roehrkasse, and R. J. Lavigne. 1975. Prey recognition by *Efferia frewingi* (Diptera: Asilidae). Ann. Entomol. Soc. Am. 68: 404–408.

Hardy, G. H. H. 1953. The prey of *Stenopogon* (Diptera, Asilidae) in New South Wales. Entomol. Mon. Mag. 89: 106.

Hassell, M. P., J. H. Lawton, and J. R. Beddington. 1976. The components of arthropod predation. I. The prey death-rate. J. Anim. Ecol. 45: 135–164.

Hocking, B. 1953. The intrinsic range and speed of flight of insects. Trans. R. Entomol. Soc. Lond. 104: 223–345.

Holdridge, L. R., W. C. Grenke, W. H. Hatheway, T. Liang, and J. A. Tosi, Jr. 1971. Forest environments in tropical life zones: a pilot study. Pergamon Press, San Francisco. 747 pp.

Ivlev, V. S. 1961. Experimental ecology of the feeding of fishes. Yale Univ. Press, New Haven. 302 pp.

Knight, D. H. 1975. A phytosociological analysis of species rich tropical forest on Barro Colorado Island, Panama. Ecol. Monogr. 45: 259–284.

Lavigne, R. J. and F. R. Holland. 1969. Comparative behavior of eleven species of Wyoming robber flies (Diptera: Asilidae). Univ. Wyo. Agric. Exp. Stn. Sci. Monogr. 18: 1–61.

Olive, C. W. 1980. Foraging specializations in orb-weaving spiders. Ecology 61: 1133–1144.

Pyke, G. H., R. H. Pulliam, and E. L. Charnov. 1977. Optimal foraging: a selective review of theory and tests. Quart. Rev. Biol. 52: 137–154.

Robinson, M. H. and B. Robinson. 1973. Ecology and behavior of the giant wood spider *Nephila maculata* (Fabricius) in New Guinea. Smithsonian Contrib. Zool. No. 149, 76 pp.

Scarbrough, A. G. 1979. Predatory behavior and prey of *Diogmites missouriensis* Bromley in Arkansas (Diptera: Asilidae). Proc. Entomol. Soc. Wash. 81: 391–400.

Scarbrough, A. G. and A. Norden. 1977. Ethology of *Cerotainia albipilosa* Curran (Diptera: Asilidae) in Maryland: Diurnal activity rhythm and seasonal distribution. Proc. Entomol. Soc. Wash. 79: 538–554.

Scarbrough, A. G. and B. E. Sraver. 1979. Predatory behavior and prey of *Atomsia puella* (Diptera: Asilidae). Proc. Entomol. Soc. Wash. 81: 630–639.

Shelly, T. E. and D. L. Pearson. 1978. Size and color discrimination of the robber fly *Efferia tricella* (Diptera: Asilidae) as a predator on tiger beetles (Coleoptera: Cicindelidae). Environ. Entomol. 7: 790–793.

———. 1980. Predatory behavior of *Proctacanthella leucopogon* (Diptera: Asilidae): Prey recognition and prey records. Environ. Entomol. 9: 7–9.

Sokal, R. R. and F. J. Rohlf. 1969. Biometry. W. H. Freeman and Co., San Francisco. 859 pp.

Taylor, L. R. 1962. The efficiency of cylindrical sticky traps and suspended nets. Ann. Appl. Biol. 50: 681–685.

Townsend, C. R. and A. G. Hildrew. 1980. Foraging in a patchy environment by a predatory net-spinning caddis larvae: A test of optimal foraging theory. Oecologia 47: 219–221.

Wallis, J. B. 1913. Robber fly and tiger beetle. Can. Entomol. 45: 135.